The role of small rodents and shrews as hosts for ticks and reservoirs of tick-borne pathogens in a northern coastal forest ecosystem

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Abstract

Ticks are important vectors for a variety of pathogens of medical and veterinary importance worldwide. Small rodents and shrews are widely distributed, and can harbour several species of ticks and substantial tick burdens. In addition they are considered important competent reservoirs for some of the most adverse tick-borne pathogens, *Borrelia burgdorferi* sensu lato causing Lyme disease and *Anaplasma phagocytophilum* causing tick-borne fever in livestock. Despite its importance, current knowledge about the small mammal-tick association from ecosystems at the northern distribution limit of ticks is scarce. In the current study I investigated the role of rodents and shrews as hosts for ticks and reservoir for tick-borne pathogens in a northern coastal forest ecosystem. I predicted that rodents and shrews would host immature life stages of *I. ricinus*, while they would host all life stages of the rodent specialist, *I. trianguliceps*. I also predicted that variation in tick burdens would be affected by extrinsic and intrinsic factors. In addition I predicted that rodents and shrews would be detected with *B. burgdorferi* s.l. and *A. phagocytophilum*. Questing ticks were sampled, and small rodents and shrews were trapped in two transects in Sogn & Fjordane, Norway, in spring and fall of 2013 and 2014. Tick burdens of different small mammal species were quantified and infestation by pathogens was determined. Distribution of questing *I. ricinus* ticks and *I. ricinus* and *I. trianguliceps* tick burdens were investigated using generalised linear mixed effect models. Rodents and shrews showed relatively high prevalence of tick infestation and some individuals carried high abundance of larvae of both *I. ricinus* and *I. trianguliceps* ticks. Both *B. burgdorferi* s.l. and *A. phagocytophilum* were detected in small mammal species. There was evidence that tick burdens were affected by extrinsic factors likely linked to local climate. Intrinsic factors were also found to affect tick burdens. Larva and nymph tick burdens were positively correlated with host body size. After controlling for body size, the residual variation in tick burdens for *I. ricinus* larvae and *I. trianguliceps* nymphs were attributed to unmeasured qualities of rodent and shrew species. The present study highlights the role of rodents and shrews as important hosts for immature stages of ticks, especially larvae. In addition this study suggests that tick burdens on rodents and shrews are affected by a complex combination of local climate and host factors, making some individuals more likely to contribute to the life cycle of ticks and the enzootic transmission cycle. To better understand tick-borne diseases in relation to climate change, the current study suggests that one must put more emphasis on intrinsic factors, since these may have major impact on the small mammals' contribution to the enzootic transmission cycle.

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1. Introduction

Ticks (Acari: *Ixodidae*) and tick-borne diseases have over the past decades become a growing concern for animal and public health in the northern hemisphere (Norman, 2004; Vorou et al., 2007; McDonald et al., 2014). Ticks are ectoparasites of terrestrial vertebrates (Hillyard, 1996) that, while taking a blood meal, are responsible for transmitting a variety of pathogenic microorganisms, such as viruses, rickettsia, spirochetes and protozoa (Jongejan and Uilenberg, 2004). Among the tick-borne pathogens that pose a public health risk, *Borrelia burgdorferi* sensu lato (s.l.), the causative agent for Lyme borreliosis (LB), is the most common (Stanek and Strle, 2003; Lindgren et al., 2006) and over the last decade there has been a significant increase in the incidence of LB in Europe (Rizzoli et al., 2011) and the United States (Bacon et al., 2008). Over 300 cases of disseminated LB have been reported annually in Norway over the past few years (The Norwegian Institute of Public Health, 2015). Another pathogen of importance is the tick-borne bacterium *Anaplasma phagocytophilum* a bacterium of special concern when it comes to infectious diseases in domestic animals in Europe. Some genetic variants of this bacterium may cause tick-borne fever (TBF) in sheep (Grøva et al., 2011), cattle (Torina et al., 2008), horses (Passamonti et al., 2010), dogs (Jensen et al., 2007) and cats (Hamel et al., 2012). TBF is one of the main scourges of the Norwegian sheep industry, as approximately 300 000 lambs in Norway are affected by TBF each year (Stuen and Bergström, 2001).

The most common vector of zoonotic pathogens (i.e. those transmitted between vertebrate hosts and humans) in Europe, *Ixodes ricinus* has expanded its range into higher latitudes and altitudes over the last decades, and increased its population densities within known endemic areas in the UK (Dobson and Randolph, 2011), in central/eastern Europe (Materna et al., 2008) and in Scandinavia (Jaenson and Lindgren, 2011; Jore et al., 2011). Previous studies have shown that the risk of contracting tick-borne diseases, such as LB, coincides approximately with the distribution and densities of *I. ricinus* (Jaenson and Lindgren, 2011; Jore et al., 2011; Sprong et al., 2012). In other words, changes in tick distribution and abundance are likely to have increased with further effect on tick related problems in Europe (Leger et al., 2013). Given the severity (e.g. economical and social costs) and the prevalence of tick-borne pathogens, an emphasis on understanding the interaction between the pathogens, their principle vector, and the reservoir hosts in natural foci is important in order to minimize the risk of human and animal infections.

The tick population dynamics and the persistence of tick-borne pathogens in natural foci are influenced by both abiotic (climate) and biotic (host availability) factors (Randolph, 2004; Pfaffle et al., 2013). *I. ricinus* is a three-host hard tick species. In general, it spends most of its life as a free-living surface dwelling parasite on the forest floor, seeking hosts, digesting blood meals, and undergoing diapause (Anderson and Magnarelli, 2008). Its population dynamics are therefore highly sensitive to the local climatic conditions like temperature, humidity and saturation deficit (Randolph and Storey, 1999; Perret et al., 2000; Tagliapietra et al., 2011). The life cycle of *I. ricinus* consists of three parasitic stages: the larva, the nymph and the adult (Hillyard, 1996; Anderson and Magnarelli, 2008), and each stage require one single blood meal before developing into the next stage, or to producing eggs. Ticks are therefore also highly dependent on the access to potential host species and their population densities to be able to fulfil their life cycle (Randolph, 2004; Gilbert, 2010; Pfaffle et al., 2013). When hosts are abundant and host communities are diverse, ticks are more likely to find appropriate hosts (Randolph, 2004; Wood and Lafferty, 2013). Hence, there is an increased chance of tick's to progress through their life cycles. Most hard ticks feed progressively on larger hosts, with larvae feeding mainly on small mammals, nymphs on small to medium sized mammals, birds and reptiles, while adults feed on vertebrates of greater size, such as ungulates (Aeschlimann, 1991). Deer and sheep can potentially feed all *I. ricinus* life stages (Handeland et al., 2013; Mysterud et al., 2014), but are especially important because the adult female ticks require hosts larger than hare for its last blood meal. Deer are therefore also referred to as "reproduction hosts" (Ruiz-Fons and Gilbert, 2010; Kiffner et al., 2010a). *I. ricinus* ticks are of special interest in the enzootic transmission cycle due to its wide range of hosts and its ability to feed on virtually any vertebrates sharing its habitat (Mehl, 1983; Mannelli et al., 2012).

The risk of contracting tick-borne diseases depends not only on the abundance of ticks, but also on the prevalence of pathogens in the tick population (Ostfeld et al., 2006). In the absence of transovarial transmission, infection in the ticks is acquired through blood meal from already infected hosts. The likelihood of an uninfected tick becoming infected therefore depends strongly on the density of available competent reservoir hosts in an area (LoGiudice et al., 2008; Pfaffle et al., 2013). The reservoir potential of a host is defined as the contribution of that particular host to the transmission of pathogens (Mather et al., 1989) and is a product of the reservoir competence of the hosts and the number of vectors fed by this individual (Schauber and Ostfeld, 2002; LoGiudice et al., 2003). However, host species differ considerably in their potential as pathogen reservoir and importance to the dynamics of

infection. For example ungulates, such as deer, feed a large number of *I. ricinus* ticks but they are not considered competent reservoir for pathogens such as *B. burgdorferi* s.l. (Mannelli et al., 2012). Small mammals, such as rodents and shrews, on the other hand are recognized as key hosts in the enzootic transmission cycle of several tick-borne pathogens causing diseases in humans and domestic animals (Mannelli et al., 2012; Ostfeld et al., 2014).

Rodents and shrews are important feeding hosts for the immature stages (larvae and nymph) of *I. ricinus* (Kiffner et al., 2010b; Bown et al., 2011) and are found to be among the most important natural competent reservoir for *B. burgdorferi* s.l. (Hanincová et al., 2003; Mannelli et al., 2012; Perez et al., 2012) and recently also for *A. phagocytophilum* (Bown et al., 2011; Majazki et al., 2013; Stuen et al., 2013). Furthermore, small mammals commonly exist at high densities and are ubiquitous animals in most forest habitats. The utilisation of small mammals by ticks has previously been investigated in forests of Europe (Paziewska et al., 2010; Bown et al., 2011; Mihalca et al., 2012), and the importance of rodents and shrews in the epidemiology of tick-borne diseases has been demonstrated (Mannelli et al., 2012; Stuen et al., 2013). Studies have however discovered that not all rodents and shrews are equally infested, and have revealed that both extrinsic (habitat, structure and microclimate) (Rosà et al., 2007; Boyard et al., 2008; Paziewska et al., 2010), seasonality and intrinsic (host species, body mass, age and sex) (Randolph, 1975a; Perkins et al., 2003; Brunner and Ostfeld, 2008a; Harrison et al., 2010; Kiffner et al., 2010b) factors are crucial to predict the individual tick burdens and how ticks are distributed across hosts. This is thought to be important for determining their reservoir potential and thus their contribution to the enzootic transmission cycle of pathogens such as *B. burgdorferi* s.l. and for *A. phagocytophilum*.

Despite the importance of the small mammal-tick association, there is limited knowledge about this association in Norway and other ecosystems at the northern distribution limit of ticks (but see; Paulauskas et al., 2008; Paulauskas et al., 2009). The knowledge about the most important small mammal reservoir for tick-borne pathogens in these ecosystems is therefore also scarce. The present study aims to gain additional insight of how important rodents and shrews are as hosts to ticks and reservoirs of tick-borne pathogens in northern coastal forest ecosystems. There will be a special emphasis on how landscape variables and host factors affect tick burdens on hosts. This includes another tick species, *Ixodes trianguliceps*. As a rodent specialist, this species may potentially serve a different role in the enzootic transmission cycle (Bown et al., 2006; Kovalevskii et al., 2013). I have quantified the tick burden on different rodent and shrew species, questing ticks in the vegetation and *B.*

burgdorferi s.l. and *A. phagocytophilum* infection rates in rodents and shrews. More specifically, I have tested the following hypotheses:

H1: The coast-inland/elevation tick abundance hypothesis

The density of ticks is commonly found to decrease with increaseing elevation and distance to the fjord (Ruiz-Fons et al., 2012; Qviller et al., 2013; Qviller et al., 2014). I therefore predict to find lower abundances of *I. ricinus* ticks questing in the vegetation with increasing elevation and distance from the fjord (H1a). Assuming a heterogeneous distribution of questing *I. ricinus*, I also predict that landscape variables will affect tick burdens on hosts. I expect *I. ricinus* tick burdens to follow the same pattern as questing *I. ricinus* (H1b). The rodent specialist *Ixodes trianguliceps* is regarded as a more robust species than *I. ricinus*, being linked to underground burrows. I therefore predict less clear patterns for *I. trianguliceps* tick burden on hosts in relation to landscape variables (H1c).

H2: The host selection-tick life stage hypothesis

Larvae and nymphs of *I. ricinus* are commonly found on small mammals, such as rodents and shrews. These mammals are regarded as too small to host adult *I. ricinus* ticks (Jaenson et al., 1994). I therefore predict to find larvae and nymphs, and no adult ticks on small mammals (H2a). And if size of host reflects choice of the different instar stages, I also predict that body size of hosts will affect the distribution of *I. ricinus* larvae and nymphs, such that the number of ticks increases with increasing body size of the hosts (H2b). The rodent specialist, *I. trianguliceps* is commonly found to parasitize small mammals during all its life stages (Randolph, 1975b; Mehl, 1983). I therefore predict to find *I. trianguliceps* larvae, nymphs and adults on small mammals (H2c), and since size of hosts seems to not reflect choice of different instar stages for this tick species, I predict that host body size will be less important for the distribution of *I. trianguliceps* ticks on hosts (H2d).

H3: The host competence hypothesis

Rodents and shrews are thought to be important natural competent reservoirs for *B. burgdorferi* s.l. (Gern and Humair, 2002) and for *A. phagocytophilum* (Stuen et al., 2013). I therefore predict to find infection of these pathogens in tissue from captured rodents and shrews.

2. Material and methods

2.1 Ethical statement

This study involves the sacrifice of small mammals, such as rodents and shrews. The study has been approved by the Norwegian Environment Agency, which regulate research with animals. There are no reasons for the rodents and shrews to suffer during this study, exceptions are risks associated with the handling that is involved in any trapping, capturing and sacrificing of small mammals.

2.2 Study area

The study area is located in the western part of southern Norway, in Førde and Askvoll municipalities in Sogn & Fjordane county (Fig. 1). The area lies mainly within the boreonemoral vegetation zone. The bedrock is dominated by gneiss, granite, and other plutonic rock types, with limited coastal areas consisting of distinctive remnants of less modified sediments, such as conglomerate and sandstone (Abrahamsen et al., 1977). The region consists of mixed forests with deciduous woodland in the south facing slopes with birch (*Betula*), alder (*Alnus incana*), grass and herbs as the dominating vegetation. Other parts are dominated by Scots pine (*Pinus sylvestris*) with elements of Norway spruce (*Picea abies*), alder and birch (Abrahamsen et al., 1977; Mysterud et al., 2002), while layers of bryophytes, lichens and heath species dominates the vegetation of the forest floor. In addition, large rough-wide marsh areas are found in the region (Abrahamsen et al., 1977). The topography consists of steep hills and mountains, with valleys, streams and fjords. The climate at the outermost areas on the coast are generally milder with higher humidity compared to the drier and colder climate higher above sea level and with increasing distance to the coast (Langvatn et al., 1996). The study area is known for its mild winter and cold summers, with an average yearly precipitation of 2270 mm and an average temperature of 6.0°C between 1961 and 1990 (Norwegian meterological station no. 57170; Norwegian Meteorological Institute, 2015).

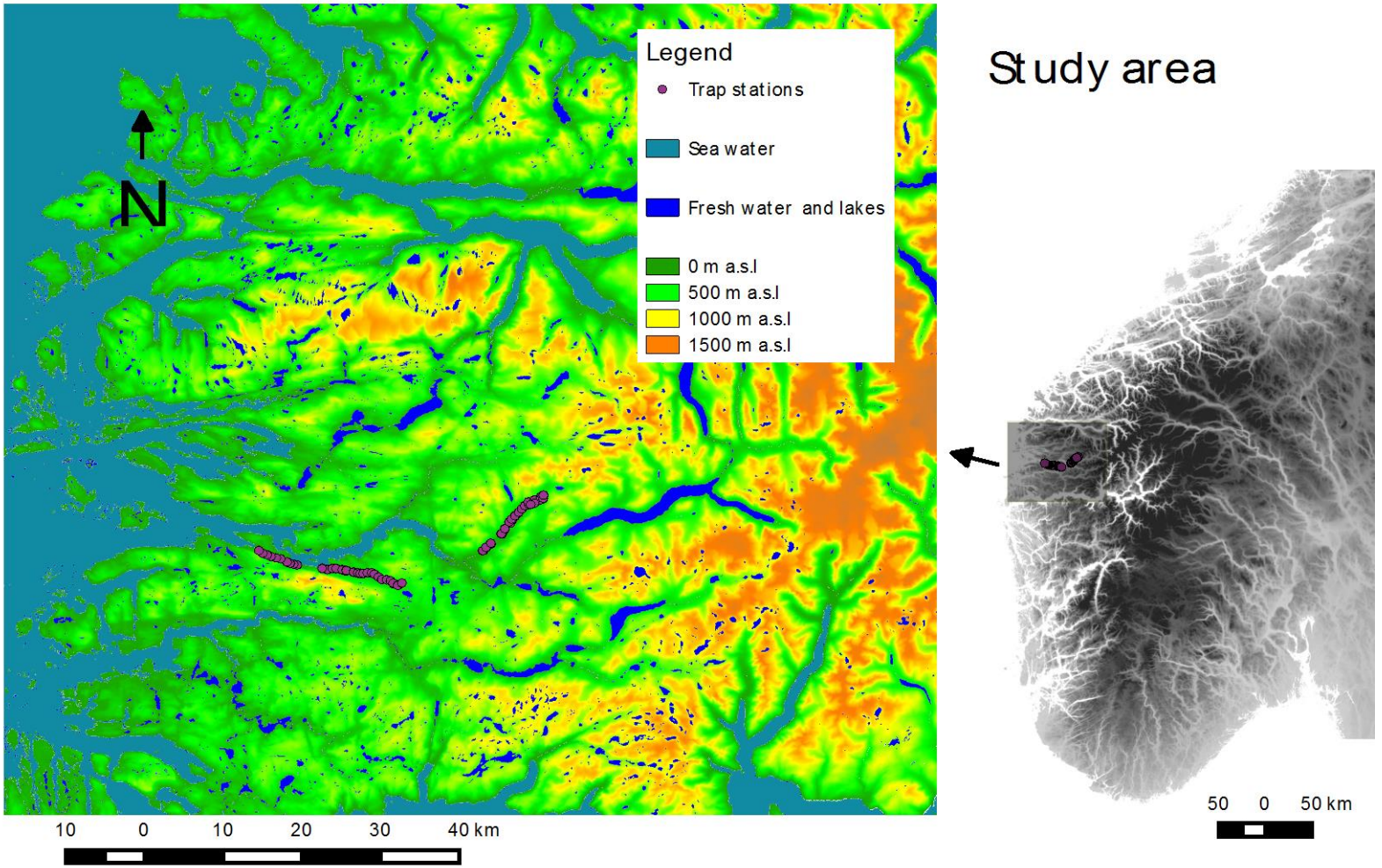

Figure 1. A map over the study area along the west coast of Norway showing the distribution of trap stations (represented in purple points) in the two transects (Angedalen and Førde west) in Sogn & Fjordane, Norway. Blue colours represent seawater, fresh water and lakes, while colours green to orange represent increasing elevation up to 1500 m a.s.l. Terrain data was calculated from a 10 m x10 m scaled digital elevation raster model (DEM), retrieved from Norge Digitalt (DEM © Kartverket; http://www.statkart.no/geonorge/norge-digitalt/).

2.3 Study design

Trapping of rodents and shrews and the flagging of ticks were done along two distinct transects during spring and fall 2013-2014. Both transects had a natural gradient from lower to higher elevation. One transect was situated in Angedalen in Førde municipality and consists of 20 trapping stations; each with four traps. The second transect was situated in the western part of Førde municipality (Førde west) and extended with 10 stations into Askvoll municipality in 2014. Therefore, the second transect consisted of 20 trapping stations in 2013 and of 30 stations in 2014. The Førde west transect was situated closer to the coast as compared to the transect in Angedalen. Stations were spread alongside the main road, minimum 50 m from the road to minimize influence from the surrounding human activity. Stations were established with at least 500 m separating them, with some natural variation due to difficulties placing stations in areas with housing and infrastructure. Stations were separated in this manner to avoid any depletion of the small mammal populations. All trap coordinates were retrieved using a handheld Garmin GPSmap 60CSx, and the landscape variables for each of these points were extracted from a 10 m x 10 m digital elevation raster model, using the GRASS GIS software (GRASS Development Team, 2013). Landscape variables that were extracted from the elevation raster model were distance to fjord, aspect of slope, slope, and elevation.

2.4 Data collection

2.4.1 Small mammals

At each station 4 traps were spaced out in the corners of a 15 m x 15 m square according to the small quadrate method (Myllymäki et al., 1971). The traps were placed in natural structures or close to holes in the ground (within 2 meters deviation from the square corner) to enhance local capture probability. A total of 436 rodents and shrews were captured (Table 1), using live trapping (Ugglan-traps) (Photo 1 and 3). All traps were baited with carrots (for water) and oats (for food) on the first day of fieldwork. Food and water reserves in all traps would allow the animals to survive for at least 24 hours (Steen et al., 2005). The traps were baited the first day, and operated for three consecutive days. All traps were controlled every day. Small mammals captured were humanly euthanized and transferred to an individual zip-lock bag, marked with station number, trap number and date. All bags were stored in a freezer for later observation.

Table 1. Number of rodent and shrew species captured (by year, by transect, by season) in Sogn & Fjordane, Norway in 2013-2014.

		Year 2013				**Year 2014**			
		Angedalen		Førde west		Angedalen		Førde west	
Species	Captured (n)	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Apodemus flavicollis	11	-	-	-	-	-	-	3	8
Apodemus sylvaticus	30	-	-	-	3	2	12	3	10
Microtus agrestis	23	-	-	-	3	1	11	1	7
Myodes glareolus	36	1	2	-	3	5	17	1	7
Neomys fodiens	3	-	-	-	-	-	2	-	1
Sorex araneus	290	1	16	1	40	2	123	4	103
Sorex minutus	38	-	5	-	2	2	6	-	23
Not identified	5	-	-	-	-	-	2	-	3
Total	**436**	**2**	**23**	**1**	**51**	**12**	**173**	**12**	**162**

2.4.2 Questing ticks

Questing *I. ricinus* were sampled at every station, once during spring and fall 2013-2014. They were sampled using the cloth-lure technique, a technique that is widely used to collect questing ticks (Vassallo et al., 2000). A towel (50 cm x 100 cm) was attached to a rod and dragged over the vegetation to simulate potential hosts for questing ticks (Photo 2). The ticks will respond to the mechanical stimuli and attach themselves to the towel (Vassallo et al., 2000). The flagging was started from the middle of one side of each sampling station, forming a 10 m long and 2 m wide (20 m^2) rectangle, directed away from the square centre. Ticks were removed from the towel, counted and identified to life stages after every 2 m of flagging. Only adults and nymphs were counted, while larval ticks were listed as present or absent. Ticks were placed into tubes with ethanol and marked with date and station number. Towels were changed after each station to avoid cross contamination. The group have considerable experience using this technique (Qviller et al., 2013). The ticks was later dried and stored in tubes with silica beads at -20 °C to preserve DNA. A total of 134 ticks were collected in the two transects (Table 2). Questing *I. ricinus* larvae were recorded as present three times in the Førde west transect.

Table 1. Number of questing *I. ricinus* ticks sampled (by transect, by year, by season) in Sogn & Fjordane, Norway in 2013-2014.

	2013		**2014**	
Transect	Spring	Fall	Spring	Fall
Angedalen	1	5	0	0
Førde west	30	20	38	40
Total (n)	**31**	**25**	**38**	**40**

Photo 1. Uggland-trap placed in natural structures (photo by Ragna Byrkjeland).

Photo 2. The equipment used in the cloth-lure technique (photo by Ragna Byrkjeland).

Photo 3. Uggland-trap baited with carrots and oats (photo by Ragna Byrkjeland).

2.5 On-host ticks and small mammal identification

All small mammals were weighed and identified morphologically to species using description by Østbye (1994). A representative subsample of animals was identified with the help from a rodent specialist, Torbjørn Håkan Ergon. From the 436 rodents and shrews that were captured, 431 animals were identified, while five animals were damaged and impossible to identify. Feeding ticks were removed from the captured rodents and shrews. All ticks (n = 1988) were identified morphologically to the life stages larva, nymph or adult, while on-host ticks from 2014 (n = 1843) were also identified to species using descriptions by Hillyard (1996). The identification of a representative subsample of ticks was checked by a tick specialist, Reidar Mehl (e.g., Mehl, 1983). Ticks were then stored in tubes with silica beads at -20 °C. The time used to investigate small mammals for ticks was set to 20 minutes for individuals captured in 2014 (n = 354), to standardise sampling effort. Investigation time was set based on experience from small mammals collected in 2013 (n = 77). Identification of on-host ticks from 2014 revealed two species of ticks, *I. ricinus* (n = 1106) and *I. trianguliceps* (n = 736). In total seven hosts species were recorded for the two tick species.

2.6 Pathogen determination

Biological material from ticks and small mammals were sent for pathogen determination at the units lab. A total of 104 questing and 44 feeding nymphs and adults tick from 77 small mammals, were determined for pathogen following a standard protocol (Mysterud et al., 2013). The protocol is based on Allender et al. (2004) with some adjustments for ticks. This procedure analyses samples for *A. phagocytophilum* and *B. burgdorferi* s.l. using real-time PCR. This involves grinding of samples using a multiplex real-time PCR assay developed by Courtney et al on a Roche Light Cycler® 480 Real-Time PCR instrument and subsequent DNA extraction. A similar protocol was used for pathogen detection in tissues from small mammals, using a piece of the ear from a total of 28 captured rodents and 73 captured shrews (Mysterud et al., 2013).

2.7 Statistics

All statistical analysis was performed using the R statistical software version 3.1.2 (R Development Core Team, 2013). To test the correlation between the variables elevation and distance to fjord I used Pearson's product moments correlation. The correlation measured the strength and direction of a linear relationship between two numerical variables. The correlation coefficient is a number between -1 and 1, the closer the value of r gets to zero, the greater the variation in the data points around the line of best fit (Whitlock and Schluter, 2009). The level of significance was set to $p < 0.05$. The weight of host species was log transformed to stabilize the variance.

The variable aspect of slope, extracted from the elevation raster model, is a circular variable that is difficult to analyse because one degree and 360 degrees is virtually the same direction. Thus, this variable was transformed into the variable northness using the sinus function of the aspect variable, which is a variable that goes from -1 (south) to 1 (north). Northness was used in the statistical analysis.

Akaike Information Criterion (AIC) was used in the model selection to determine the best model (Burnham and Anderson, 2004). AIC uses deviance as a measure of fit, it finds the most parsimonious models as a balance between variation explained by the model and number of parameters included. By adding parameters this criterion adds a term to penalize more complex models (Bolker et al., 2009).

2.7.1 Generalized mixed effect models

There are in general two main challenges related to the analysis of tick abundance data. Firstly, the distributions of parasites are often overdispersed, meaning that the variance exceeds the mean ($\mu<\sigma^2$). Their distribution will, therefore often be better represented using a negative binomial distribution, that allows for mean and variance to be different (Shaw and Dobson, 1995). The fit of the negative binomial distribution was confirmed by model selection using AIC, as suggested by Zuur et al. (2009). In addition, tick abundance data may have higher proportion of zeros than what is expected from a negative binomial distribution, warranting the use of zero-inflated models (Zuur et al., 2009). Secondly, there are challenges related to the sampling design with four traps in each station. The variation within station was expected to be smaller than the variation between stations. This violates the assumption of independent observations, and can be handled statistically with the inclusion of random effects. The questing tick abundances and tick burdens were analysed with generalized mixed

effect models using the library "glmmADMB" in R (Skaug et al., 2011). This library was used to handle negative binomial data and enable incorporation of random effects (Bolker et al., 2009; Skaug et al., 2011). Several models were developed, using backward and forward model selection, to investigate questing tick abundance data and tick burden on small mammal data. The model selection confirmed that models including a zero-inflated negative binomial distribution did not give the best fit.

2.7.2 Questing ticks

Firstly, a model was built to test the cost-inland/elevation hypothesis (H1a), to get a better understanding of factors affecting the distribution of questing ticks in the landscape. Data from Angedalen was excluded because only 6 ticks were found there. Questing *I. ricinus* ticks from both years (2013 – 2014), from the Førde west transect (n =128) was included in the analyses. The most parsimonious model was found by removal of covariates from a full model in a backward model selection procedure. The full model included distance to fjord, elevation, slope, northness, season (spring/fall), year (2013/2014), host abundance (No. captured at trap site) and interactions with season as fixed effects. Number of nymphs and adults pooled was used as the response variable, as the total sample size was relatively small. Only one flagging was performed in each trap station, and random term was therefore not used in this model.

2.7.3 Tick burdens on small mammals

Secondly, models were built to test how tick burdens on small mammals are affected by extrinsic (H1b and c) and intrinsic factors (H2b and d). Small mammals from 2014 from both transects were used in these analyses, as sample size from 2013 was very low. One species of shrew (*Neomys fodiens*) was excluded due to low sample size (n = 3). Number of observations in all models built for tick burdens was 351 (number of small mammals). Both tick species and each of the life stages larva and nymph were modelled in four separate analyses. The full models included host species, body weight of host species, elevation, distance to fjord, slope, northness, transect (Angedalen/Førde west) and season (spring/fall) as fixed effects. In addition, interactions between transect and two other covariates (elevation and distance to fjord) were added as fixed effects in the model selection for both tick species for the larva life stage. All models used number of ticks as the response variable. I chose a

backward selection procedure, except in the case of *I. ricinus* nymphs. Only 10 small mammals were parasitized with *I. ricinus* nymphs, and the limited variability in the dataset gave no significant random terms. I chose a forward model selection in this case, because a large number of parameters would be superfluous, and the exclusion of random terms allow for a forward model selection.

3. Results

3.1 Questing ticks

A total of 118 nymphs and 10 adult questing *I. ricinus* were captured in the Førde west transects in May/June and September of 2013-2014. The density of *I. ricinus* in the vegetation was best predicted by the model including the variables elevation and northness as predictors (Table 3). The variables distance to fjord, slope, season, year, host density and interaction terms did not entered the most parsimonious model (see appendix A). The abundance of questing *I. ricinus* decreased significantly with increasing elevation (Fig. 2A). The pattern is hence consistent with the coast-inland/elevation tick abundance hypothesis (H1a). In addition the abundance of *I. ricinus* were significantly lower in more north-facing stations (Fig. 2B). Distance to fjord was positively correlated with elevation ($r_{Pearson's} = 0.88$, $p < 0.001$), meaning that higher elevation coincide with a longer distance from the fjord.

Table 3. Estimates from the top ranked model explaining variation in abundance of questing ticks as a function of landscape variables in Førde west, Sogn & Fjordane county for 2013 and 2014. SE = standard error.

Parameter	**Estimate**	**SE**	**z**	**p**
Intercept	1.93	0.51	3.78	0.00015
Elevation	-0.010	0.0027	-3.89	0.00010
Northness	-0.72	0.29	-2.48	0.013

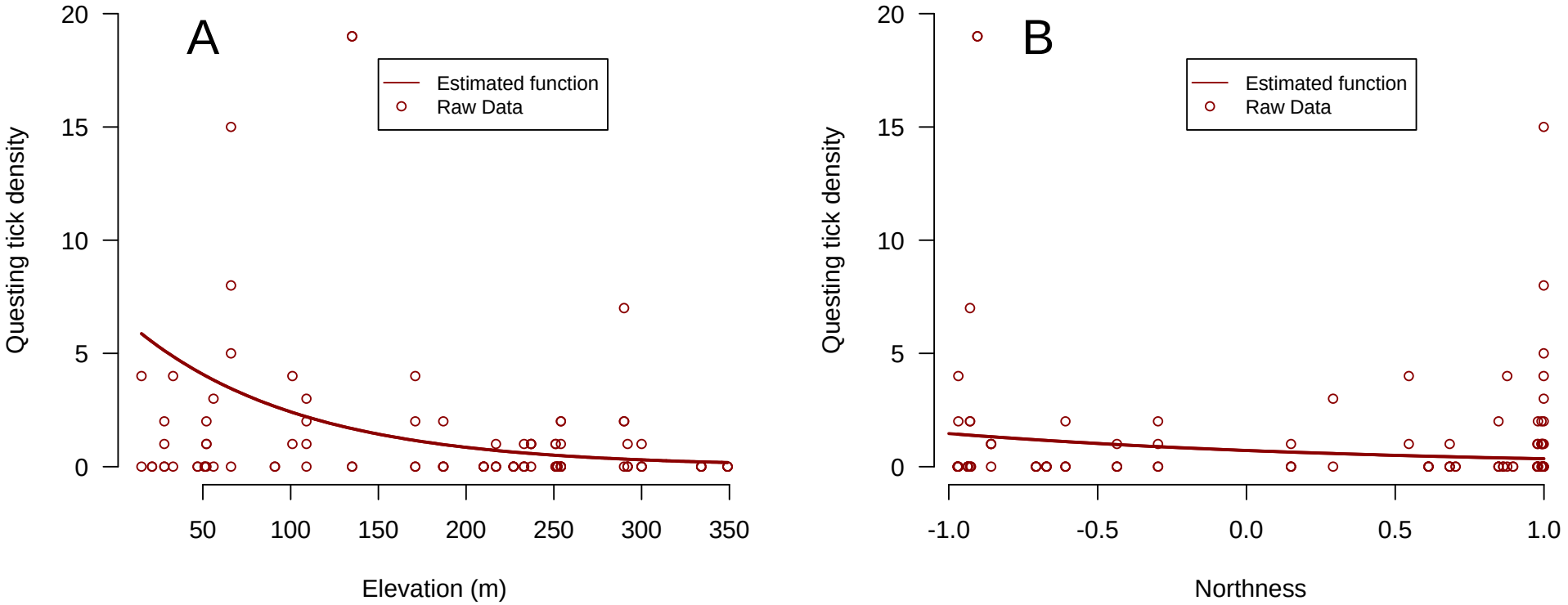

Figure 2. Questing tick density as a function of A) elevation (meters above mean sea level), predicted for northness = 0 (east or west), and B) northness (-1 = south, 1 = north, 0 = east or west) predicted for median elevation in the Førde west transect, Sogn & Fjordane county. Raw data represent all questing ticks collected (n = 128).

3.2 Tick burdens on small mammals

From the total of 351 examined animals included in these analyses, 71.7% were infested with ticks. The total number of ticks collected from the infested hosts was 1827. The two tick species that were identified had similar overall on-host infestation prevalence. *I. ricinus* was found on 51.6 % of all hosts, while *I. trianguliceps* was found on 52.4% of all hosts. A total of 114 (45.2% of all hosts with ticks) hosts had polyspecific parasitism with both species of ticks. For the analysis of tick burdens on small mammals the two variables elevation and distance to fjord were positively correlated ($r_{Pearson's} = 0.62$, $p < 0.001$). This means that an intrinsic effect of the two variables may be masked by this correlation.

3.2.1 *Ixodes ricinus* burdens on rodents and shrews

I. ricinus was the dominant ticks species collected from host animals and made up 60.2% of all ticks collected (total n = 1827). The majority of *I. ricinus* collected were larvae (98.2%, total n = 1100) with a median intensity of 3.0 ticks and a range of 1 - 104 ticks on hosts (Table 4). Nymphs were only represented in a small number (1.82%, total n =1100), with a median intensity of 1.0 ticks and a range of 1 - 9 ticks on hosts. No adult *I. ricinus* was found. The pattern is hence in accordance with the host selection-tick stage life hypothesis (H2a). *I. ricinus* larvae were recorded on six host species, while four host species were recorded for *I. ricinus* nymphs.

Table 4. Prevalence and intensity (mean, median and range) of *Ixodes ricinus* tick parasitism in rodents and shrews by host species, in Sogn & Fjordane, Norway in 2014. Prevalence (percent of animals infested), intensity (the mean and middle number of ticks abundance among infested animals. Range is the smallest interval including all data of tick abundance among infested animals) (* = the range is one).

		Larvae					Nymph				
				Intensity					Intensity		
Host	**Examined (n)**	**With (n)**	**Prevalence (%)**	**Mean**	**Median**	**Range**	**With (n)**	**Prevalence (%)**	**Mean**	**Median**	**Range**
Apodemus flavicollis	11	3	27.3	4.0	5	1 - 6	-	-	-	-	-
Apodemus sylvaticus	27	14	51.9	15.9	4	1 - 104	2	7.41	1.50	1.5	1 - 2
Microtus agrestis	20	11	55.0	4.27	3	1 - 20	4	20.0	3.00	1.0	1 - 9
Myodes glareolus	30	25	83.3	4.72	4	1 - 23	2	6.67	1.00	1.0	1*
Sorex araneus	232	122	52.6	5.51	3	1 - 63	2	0.860	1.50	1.5	1 - 2
Sorex minutus	31	5	16.1	1.80	1	1 - 5	-	-	-	-	-
Total	**351**	**180**	**51.3**	**6.00**	**3**	**1 - 104**	**10**	**2.85**	**2.00**	**1**	**1 - 9**

The burdens of *I. ricinus* larvae on rodents and shrews were best explained by the model including the variables host species, body weight of host, distance to fjord, northness, slope and season (Table 5). The variables elevation, transect and interaction terms were not included in the most parsimonious model (see appendix B). Distance to fjord had significant effect on the burdens of *I. ricinus* larvae on rodents and shrews, with decreasing numbers of *I. ricinus*, as the distance to the fjord increased (Fig. 3A). This was expected from the coast-inland/elevation tick abundance hypothesis (H1b). Additionally, there were lower tick burdens on hosts captured at more north-facing stations (Fig. 3B) and higher tick burdens during fall (September) compared to the spring (May/June) of 2014. Lastly, the burdens of ticks increased significantly with increasing body weight of hosts (Fig. 5), as expected from the host selection – tick life stage hypothesis (H2b).

Table 5. Estimates from the top ranked model explaining variation in *I. ricinus* larvae burdens on rodents and shrews as a function of landscape variables and host factors in Sogn & Fjordane, Norway in 2014. Season and host species are factor variables. Baseline for host species is *Sorex araneus*. Baseline for season is fall. The model included station as a random term. SE = standard error.

Parameter	**Estimate**	**SE**	**z**	**p**
Intercept	-2.22	0.996	-2.23	0.026
Apodemus flavicollis	-1.69	0.88	-1.92	0.055
Apodemus sylvaticus	-0.015	0.48	-0.03	0.97
Microtus agrestis	-1.79	0.69	-2.60	0.0093
Myodes glareolus	-0.52	0.53	-0.99	0.32
Sorex minutus	-1.57	0.65	-2.42	0.016
Log (weight)	1.38	0.44	3.16	0.0016
Distance to fjord	-0.00013	0.000045	-2.84	0.0045
Slope	0.025	0.014	1.77	0.077
Northness	-0.49	0.24	-2.02	0.043
Season Spring	-0.92	0.37	-2.48	0.013

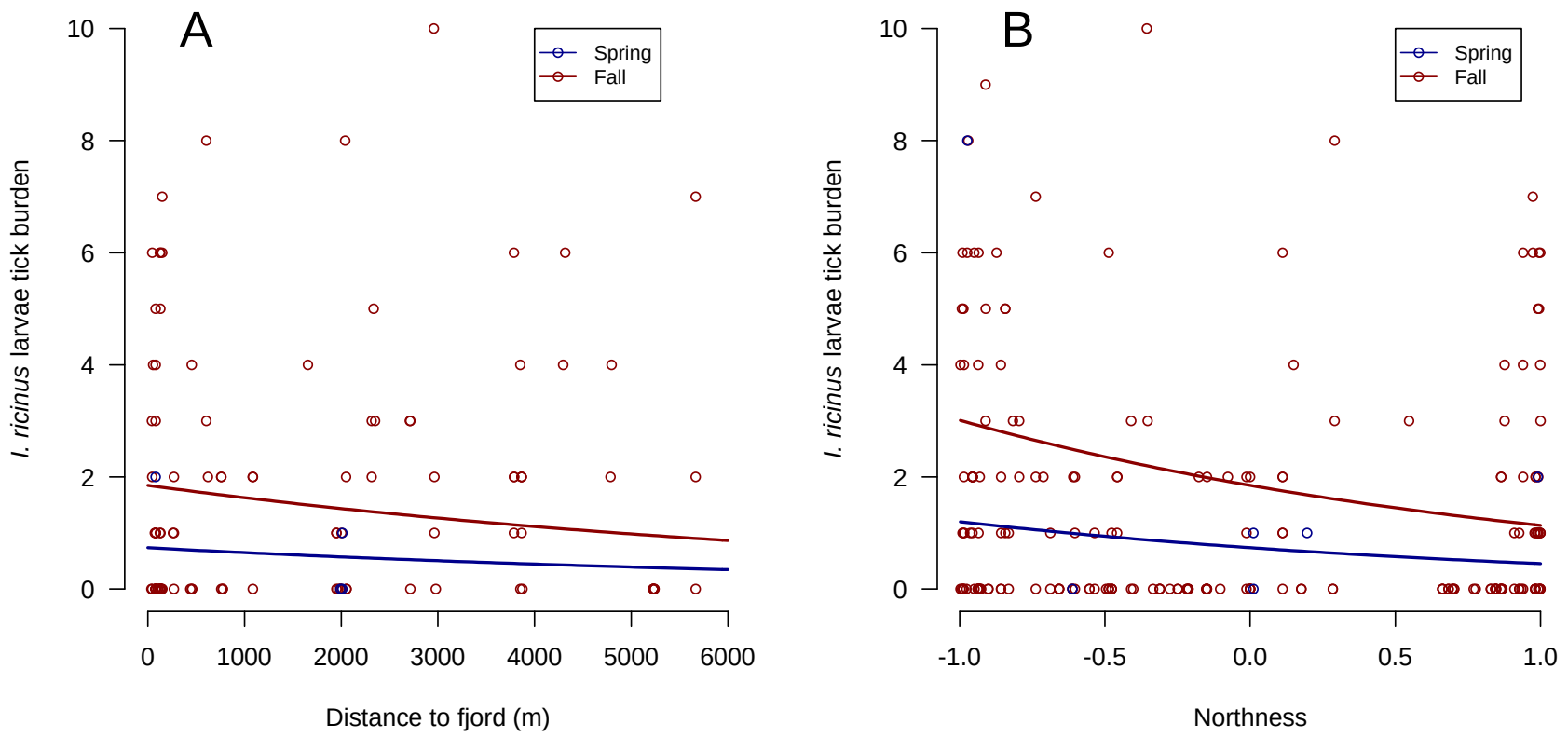

Figure 3. Burden of I. *ricinus* larvae as a function of A) distance to fjord and B) northness (-1 = south, 1 = north, 0 = east or west) in Sogn & Fjordane, Norway in 2014. The lines are estimated for the shrew species *Sorex araneus* for fall and spring 2014 (n = 232). The lines are predicted for the mean body weight (g) of the same species. All raw data are not presented as they are outside the range chosen for the y-axis (Table 4).

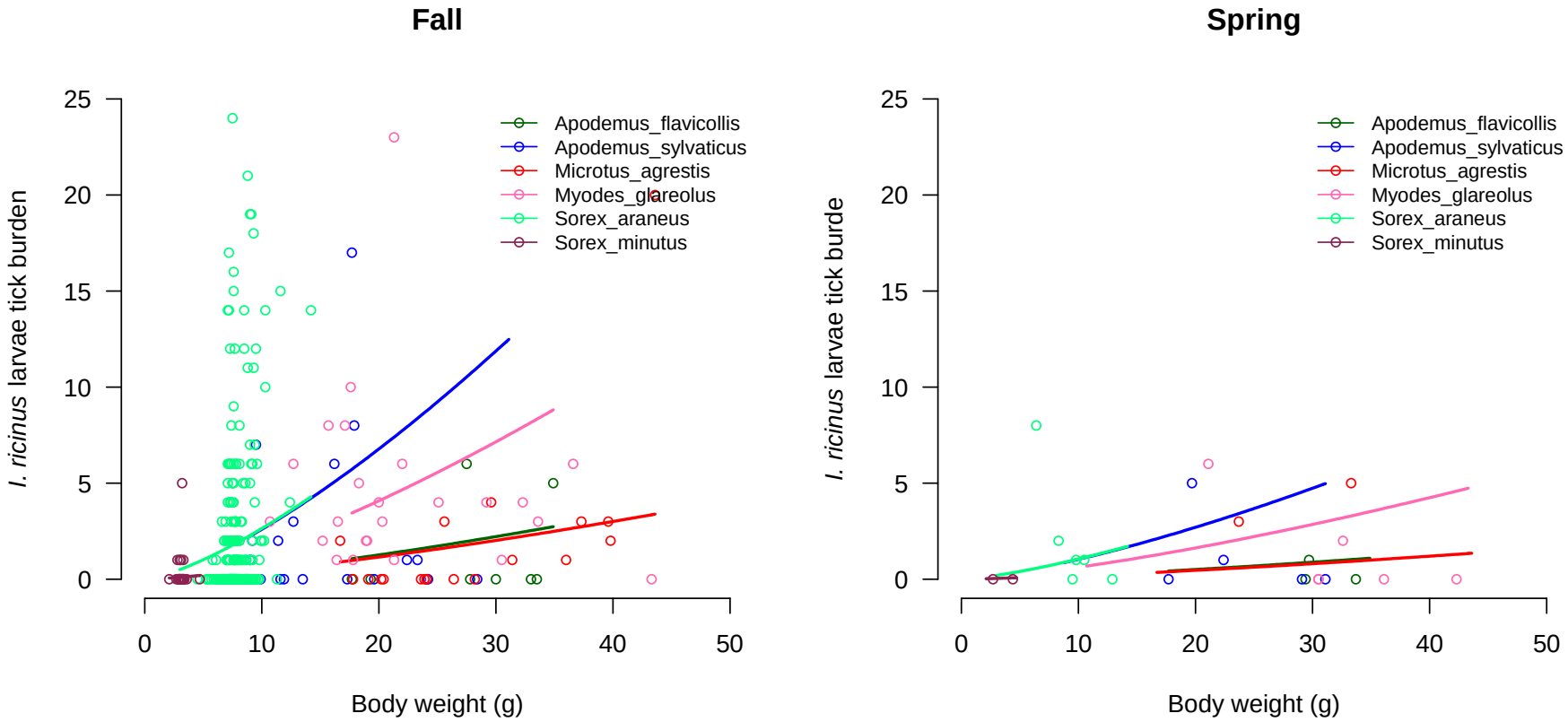

Figure 4. Burden of *I. ricinus* larvae on rodents and shrews (n = 351) as a function of host body weight (g), in Sogn & Fjordane, Norway in spring and fall 2014. Lines are estimated for each host species, within the range of observed body weights (g) for host species. All raw data are not presented in these figures as tick counts are outside the range chosen for the y-axis (Table 4).

The burdens of *I. ricinus* nymphs on rodents and shrews were best explained by the model included the variable body weight of hosts (Table 6). The variables host species, elevation, distance to fjord, slope, northness, transect and season were not included in the most parsimonious model (see appendix C). Tick burdens increased significantly, with increasing body weight of the hosts (Fig. 5), as expected from the host selection-tick life stage hypothesis (H2b).

Table 6. Estimates from the top ranked model explaining variation in *I. ricinus* nymph burdens on rodents and shrews as a function of host factor in Sogn & Fjordane, Norway in 2014. SE = standard error.

Parameter	**Estimate**	**SE**	**z**	**p**
Intercept	-9.31	1.76	-5.30	< 0.0001
Log (weight)	2.36	0.62	3.83	0.00013

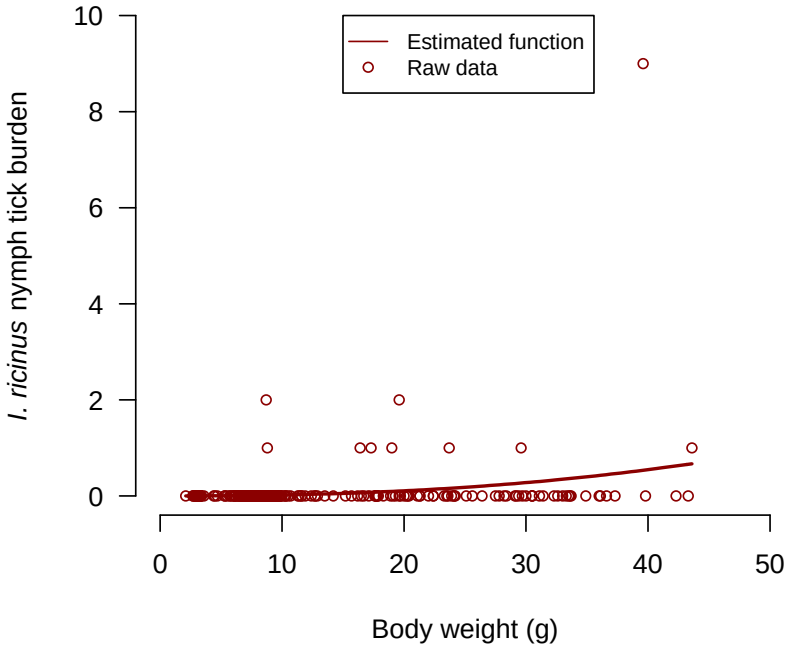

Figure 5. Burden of *I. ricinus* nymphs on rodents and shrews (n = 351) as a function of host body weight (g), in Sogn & Fjordane, Norway in 2014. The line is estimated within the range of observed body weight for all rodents and shrews. All raw data is presented in the figure (Table 4).

3.2.2 *Ixodes trianguliceps* burdens on rodents and shrews

I. trianguliceps made up about 39.7% of all ticks collected (total n =1827) from rodents and shrews. The majority of *I. trianguliceps* collected were larvae (91.3%, total n = 727), with a median intensity of 2.0 and a range of 1 - 25 ticks on hosts (Table 7). *I. trianguliceps* nymphs were represented in a slightly higher number than *I. ricinus* nymphs (8.67%, n = 727), with a median intensity of 1.0 and a range of 1 - 13 ticks on hosts. One adult *I. trianguliceps* was found. The pattern was consistent with the host selection-tick life stage hypothesis (H2c). *I. trianguliceps* larvae were recorded on six different host species, while nymphs were recorded on five different host species.

Table 7. Prevalence and intensity (mean, median and range) of *I. trianguliceps* tick parasitism in rodents and shrews by host species in Sogn & Fjordane, Norway in 2014. Prevalence (percent of animals infested), intensity (the mean and middle number of ticks abundance among infested animals. Range is the smallest interval including all data of tick abundance among infested animals) (* = the range is one).

		Larvae					Nymph				
				Intensity					Intensity		
Host	**Examined (n)**	**With (n)**	**Prevalence (%)**	**Mean**	**Median**	**Range**	**With (n)**	**Prevalence (%)**	**Mean**	**Median**	**Range**
Apodemus flavicollis	11	8	72.7	2.38	1.5	1 - 6	3	27.3	1.00	1.00	1*
Apodemus sylvaticus	27	16	59.3	4.19	2.5	1 - 15	2	7.41	1.50	1.5	1 - 2
Microtus agrestis	20	12	60.0	3.58	1.5	1 - 17	2	10.0	1.00	1.0	1*
Myodes glareolus	30	18	60.0	3.56	2.5	1 - 14	6	20.0	1.30	1.0	1 - 2
Sorex araneus	232	115	49.6	3.79	3.0	1 - 25	18	7.76	2.62	1.0	1 - 13
Sorex minutus	31	6	19.4	5.83	2.0	1 - 17	-	-	-	-	-
Total	**351**	**175**	**49.9**	**3.70**	**2**	**1 - 25**	**31**	**8.83**	**2.00**	**1**	**1 - 13**

The burdens of *I. trianguliceps* larvae on rodents and shrews were best explained by the model including the variables body weight of hosts, elevation, slope and season (Table 8). The variables host species, distance to fjord, northness, transect and interaction terms were not included in the most parsimonious model (see appendix D). Elevation had significant effect on the burden of *I. trianguliceps* larvae on rodents and shrews, with decreasing numbers of *I. trianguliceps*, as the elevation increased (Fig. 6B). This model differed from and is not as detailed as for *I. ricinus*. The result is thus partly as expected from the coast-inland/elevation tick abundance hypothesis for *I. trianguliceps* (H1c). In addition, there were significant differences between the two seasons, with a lower tick burden during the fall (September) compared to the spring (May/June) in 2014. Tick burdens also increased with increasing body weight of hosts in the top ranked model (Fig. 6A). The relationship was however not significant ($p = 0.052$), possibly suggesting a weak support for the host selection-tick life stage hypothesis (H2d).

Table 8. Estimates from the top ranked model explaining variation in *I. trianguliceps* larvae burdens on rodents and shrews as a function of landscape variables and host factors in Sogn & Fjordane, Norway in 2014. Season is a factor variable. Baseline for season is fall. The model included station as a random term. SE = standard error.

Parameter	**Estimate**	**SE**	**z**	**p**
Intercept	-0.81	0.59	-1.36	0.18
Log (weight)	0.35	0.18	1.94	0.052
Elevation	-0.0032	0.0015	-2.16	0.031
Slope	0.049	0.012	3.99	< 0.0001
Season Spring	1.31	0.35	3.73	0.00019

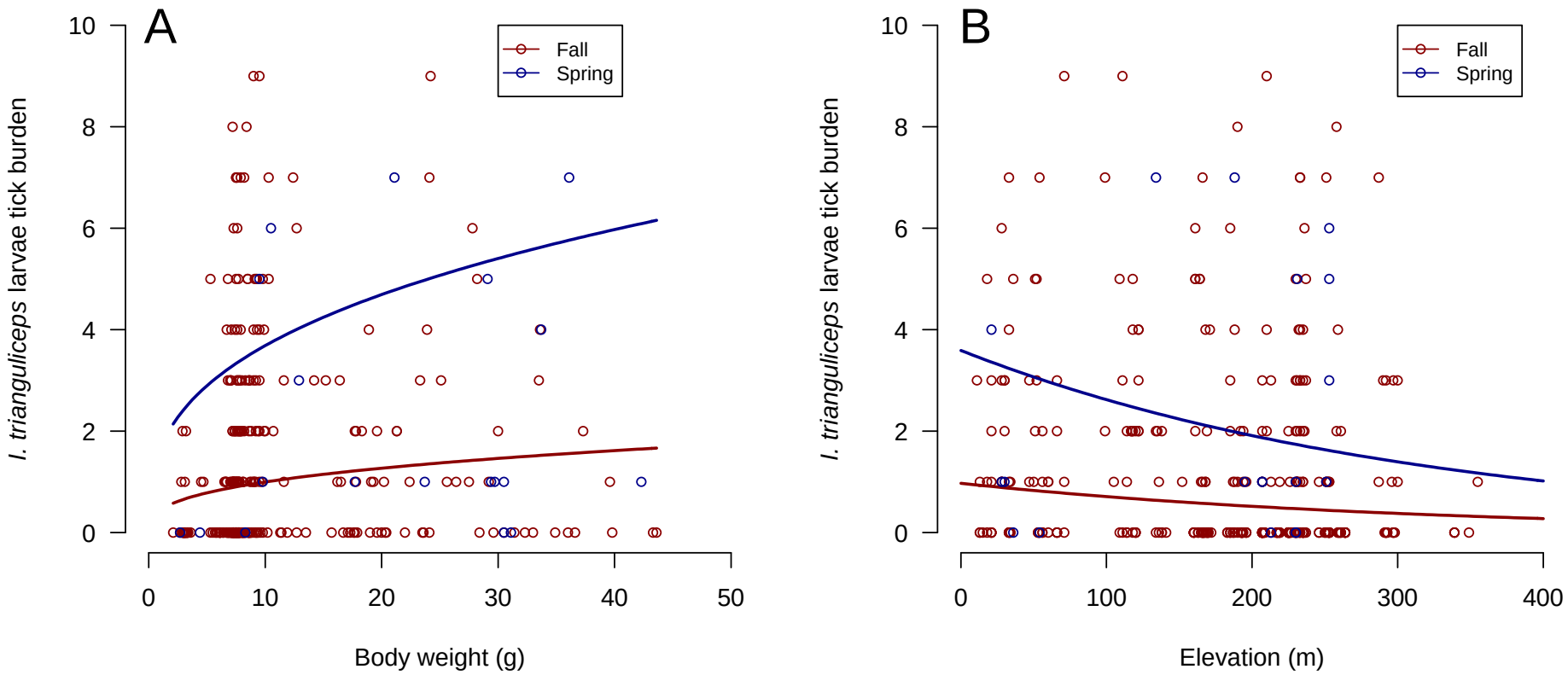

Figure 6. Burden of *I. trianguliceps* larvae on rodents and shrews (n = 351) as a function of A) host body weight (g) and B) elevation (measured as meters above sea level), in Sogn & Fjordane, Norway in 2014. A) Lines are predicted within the range of observed body weight of host species. B) The lines are predicted with the mean weight (g) of hosts. All raw data are not presented in these figures as numbers of ticks on certain small mammal species are outside the range chosen for the y-axis (Table 7).

The burdens of *I. trianguliceps* nymph on rodents and shrews were best explained by the model including the variables host species, body weight of hosts and transect (Table 9). The variables elevation, distance to fjord, slope, northness, season and interaction terms were not included in the most parsimonious model (see appendix E). There were significant differences between the two transects, with higher tick burdens on rodents and shrews captured in Førde west at the coast compared to Angedalen further inland. Lastly, the tick burdens also increased with increasing body weight of hosts in the top ranked model (Fig. 7). The relationship was not significant (p = 0.052), and the estimate was smaller than for *I. ricinus*, possibly suggesting a weak support for the host selection-tick life stage hypothesis (H2d). The estimate for *S. minutus* is very uncertain. This is because there was no nymphs found on this host species.

Table 9. Estimates from the best model explaining variation in *I. trianguliceps* nymph burdens on rodents and shrews as a function of landscape variables and host factors in Sogn & Fjordane, Norway in 2014. Transect is a factor variable. Baseline for transect is Angedalen. The model included station as a random term. SE = standard error.

Parameter	**Estimate**	**SE**	**z**	**p**
Intercept	-7.23	1.96	-3.69	0.00022
Apodemus flavicollis	-3.84	1.38	-2.78	0.0055
Apodemus sylvaticus	-1.12	1.09	-1.03	0.30
Microtus agrestis	-1.78	1.48	-1.20	0.23
Myodes glareolus	-0.65	1.20	-0.54	0.59
Sorex minutus	-20.7	33879	0.00	1
Log (weight)	1.70	0.88	1.94	0.052
Transect Førde west	1.49	0.64	2.35	0.019

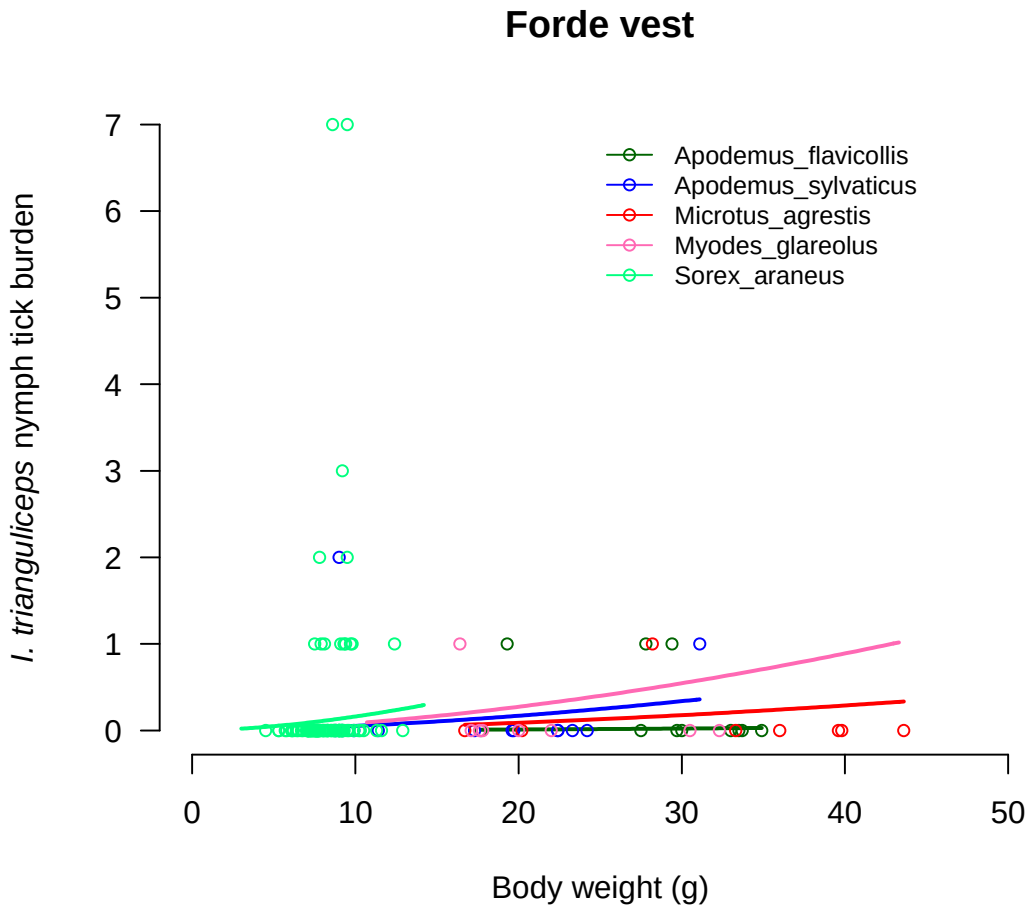

Figure 7. Burden of *I. trianguliceps* nymphs on rodents and shrews (n = 351) as a function of host body weight (g) in the Førde west transect, in Sogn & Fjordane, Norway in 2014. Lines are estimated for each host species, within the range of observed body weight for host species. All raw data are not presented in the figure as some tick counts are outside the range chosen for the y-axis (Table 7).

3.3 Prevalence of tick-borne pathogens

A total of 101 rodents and shrews were assessed for presence of tick-borne pathogens. The presences of both pathogens were detected in the tissue samples from both the rodents and the shrews. This was expected in the host competence hypothesis (H3). 14.85% (n = 101) of animals were positive for *A. phagocytophilum*, while 6.93% (n = 101) were positive for *B. burgdorferi* s.l. (Fig. 8). The two pathogens were detected in three different host species. *M. agrestis* (1), *M. glareolus* (2) and *S. araneus* (4) were infected with *B. burgdorferi* s.l., while *M. glareolus* (2) and *S. araneus* (13) were both infected with *A. phagocytophilum*.

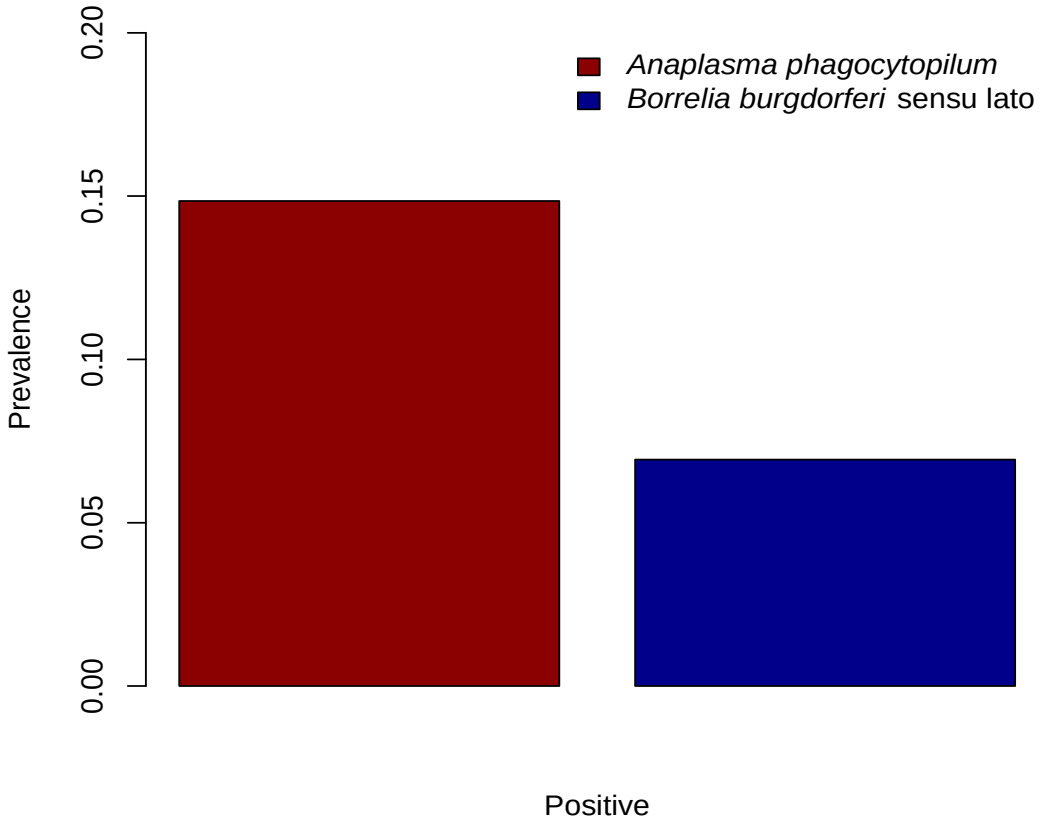

Figure 8. Prevalence of *A. phagocytophilum* and *B. burgdorferi* s.l. in rodents (n = 28) and shrews (n = 73) in Sogn & Fjordane, Norway in 2013 - 2014.

4. Discussion

Increased knowledge of the tick-host ecology at the northern distribution limit of ticks is important in a time where climate is assumed to become more favourable for ticks and hosts in northern ecosystems (Jaenson and Lindgren, 2011; Porretta et al., 2013; Ostfeld and Brunner, 2015). Knowledge can provide new perspectives and influence our understanding of the infection risks associated with tick-borne diseases. The primary purpose of this study was to assess the relative importance of small rodents and shrews as hosts for ticks at their northern distribution limit. I predicted that variations in questing tick abundance and individual tick burdens could be explained by landscape variables (extrinsic) and host factors (intrinsic). In the present study rodents and shrews were mainly found to host larvae and nymphs *I. ricinus* and *I. trianguliceps* ticks. However there were variations in tick burdens within and between rodent and shrew species. As predicted from the coast-inland/elevation hypothesis (H1), questing tick abundances decreased with increasing elevation. Tick burdens were also found to decrease with increasing elevation and distance to the fjord. In addition, tick burdens increased with increasing body size, as predicted by the host selection-tick life stage hypothesis (H2). Lastly, I detected infection of tick-borne pathogens in both rodents and shrews, as predicted by the host competence hypothesis (H3).

4.1 Distribution of ticks in the landscape

Ticks in the Ixodid complex are intermittent parasites, which means that they tend to spend as much as 98% of their life cycle as free living within their habitat (Anderson and Magnarelli, 2008). This makes them highly sensitive to climate. Questing is the behaviour where the ticks leave the ground microhabitat and climb up vegetation in order to find an appropriate host. This behaviour is essential for ticks and their feeding biology (Anderson and Magnarelli, 2008), and it is this behaviour that puts humans and domestic animals at risk for parasitism and pathogen infection. *I. ricinus* ticks have certain temperature and humidity requirements, which is essential for questing, development and survival (Randolph and Storey, 1999; Perret et al., 2000; Tagliapietra et al., 2011). Climate parameters are therefore thought to be the principal factors limiting the geographical range of the species (Lindgren et al., 2000; Gray et al., 2009).

Temperature has been shown to be a strong landscape-dependent climate variable (Gilbert, 2010), and decreases with increasing elevation globally. It is therefore possible to

study the onset of questing, tick phenology and questing tick abundance under different climatic regimes, only by moving a short distance along an elevation gradient. As predicted by the coast-inland/elevation tick abundance hypothesis (H1a) I observed that the abundance of questing *I. ricinus* ticks decreased with increasing elevation (Fig. 2A) on the west coast of Norway, most likely because of the decrease in temperature with increasing elevation. Colder temperatures at higher elevations have been shown to limit or prevent tick establishment and development (Daniel, 1993). The current results is in line with several recent studies on questing tick abundance from Switzerland (Jouda et al., 2004), Norway (Qviller et al., 2014) and the UK (Gilbert, 2010). These have shown that ticks at higher elevations have a fairly short questing season compared to the ticks in the lowland, and that there are decreases in tick abundance with increasing elevations. Questing activity of *I. ricinus* is limited by low temperatures, and very few ticks quest at temperatures below 5°C at the western coast of Norway (Qviller et al., 2014). However, since *I. ricinus* occupies such wide latitudinal and altitudinal ranges (Randolph et al., 2002) over which temperature conditions are likely to vary, it is expected that *I. ricinus* will adapt and show variation in the response to temperature with local effects on questing tick density, onset of questing and seasonal activity among other behaviours (Randolph, 2004; Cadenas et al., 2007). A recent experimental study has revealed that *I. ricinus* shows adaptations in questing behaviour to different local thermal climates (Gilbert et al., 2014).

Although tick abundances have been reported to decrease with increasing elevation on several occasions, there are some studies that have revealed contrasting results. Both Burri et al. (2007) and Cadenas et al. (2007) found that the questing ticks densities were highest at the most elevated locations in north-facing slopes. This might be expected in a region that tends to be relatively hot and dry at the lower elevation during summer, making elevated north-facing locations a more favourable humid microclimate for ticks in continental Europe (Burri et al., 2007; Cadenas et al., 2007). This is, however, not the case on the west coast of Norway, where humidity has been shown to be no limitation for questing ticks (Qviller et al. 2014), and where summers still are relatively cold. This was also supported by the fact that I observed lower abundance of questing *I. ricinus* at higher elevations, after controlling for the degree of northern exposure (the northness variable). I found an overall higher abundance of *I. ricinus* in the south-facing stations (Fig. 2B). In the present study it seems likely that much of the effects of elevation and northness on the distribution of questing ticks are linked to local climate, with temperature probably playing an important role.

4.2 Distribution of tick life stages on small mammal hosts

Hosts are important for the survival and fulfilment of tick life cycles; regardless of the short time ticks spend on them (Randolph, 1979; Shaw et al., 2003). Ticks are found to rely on the availability of rodents and shrews during parts or all of their life cycle (Randolph, 1975b; Paulauskas et al., 2009; Harrison et al., 2010; Paziewska et al., 2010; Bown et al., 2011). However, not all rodents and shrews are equally parasitised by ticks. A key element in understanding individual hosts' contribution to the tick life cycle and the maintenance of the enzootic transmission cycle is to understand how ticks are distributed among their hosts. Ticks are similar to other macroparasites, often aggregated on their hosts (Shaw and Dobson, 1995). This distribution thus results in a few hosts feeding many ticks, while many hosts feed very few ticks. More importantly, it implies that each individual host will contribute differently to the dynamics of transmission, and the transmission of tick-borne pathogens will be focused on a small proportion of the host population (Woolhouse et al., 1997; Perkins et al., 2003). The variation in tick burdens on hosts is the outcome of natural causes, and is often a combination of extrinsic factors (Randolph and Storey, 1999; Rosà et al., 2007; Boyard et al., 2008; Paziewska et al., 2010), seasonality and intrinsic factors (Brunner and Ostfeld, 2008a; Harrison et al., 2010; Kiffner et al., 2010b).

4.2.1 Small mammals as hosts for *I. ricinus* and *I. trianguliceps*

The current study supports previous findings that rodents and shrews are hosts for *I. ricinus* and *I. trianguliceps* ticks (e.g. Nilsson, 1974; Matuschka et al., 1991; Humair et al., 1993; Paulauskas et al., 2009; Bown et al., 2011; Mihalca et al., 2012; Perez et al., 2012; Kovalevskii et al., 2013). Rodents and shrews were found to be hosts for larva and nymph stages of *I. ricinus*, but I did not find any adult *I. ricinus* on small mammals. This was as expected from the host selection-tick life stage hypothesis (H2a). *I. ricinus* is a host generalist (Mehl, 1983), and adults mainly feed on larger hosts, such as ungulates. However, the role of rodents and shrews as important natural hosts for larva and nymph *I. ricinus* is well established (e.g. Sinski et al., 2006; Bown et al., 2011; Mihalca et al., 2012; Martello et al., 2014). This study clearly revealed that larvae, more frequently than nymphs infested the small mammal population on the west coast of Norway (Table 4). The predominantly infestation of *I. ricinus* larvae on small mammals has been observed among small mammals previously in studies from Germany (Matuschka et al., 1991), France (L'Hostis et al., 1996), Romania (Mihalca et al., 2012), and Poland (Sinski et al., 2006). The most likely explanation

for this is that the nymph life stages attach to other hosts in the system, mainly due to their questing behaviour. Nymphs quest higher in the vegetation compared to larvae and thus are less likely to encounter small mammals that move through the litter layer (Matuschka et al., 1991; Randolph and Storey, 1999). The collection of ticks from host species other than small rodents and shrews would provide useful and complementary information in the future.

All life stages of *I. trianguliceps* were found on rodents and shrews, as expected by the host selection-tick life stage hypothesis (H2c). This tick species is known to utilise small mammalian hosts throughout all its life stages (Randolph, 1975b; Mehl, 1983). Proportionally *I. trianguliceps* larvae parasitised host species more frequently than nymphs and adults (Table 7). Only one adult *I. trianguliceps* was detected. The lower abundance of *I. trianguliceps* nymphs and adults has been observed in several studies previously (e.g. Bown et al., 2011; Kovalevskii et al., 2013). These results are though not consistent with the ecology of *I. trianguliceps*. This species lives mainly in the nest and/or burrows of its small mammalian hosts and does not quests on the vegetation (Randolph, 1975b). Encounter with other hosts in the system is less likely. Thus, the main explanation for the higher level of larvae attachment is thought to be post larva/nymph mortality. This may of course also contribute to the predominantly infestation of *I. ricinus* larvae on hosts.

In the current study small mammals showed relatively high overall infestation prevalence of larval ticks (Table 4 and 7) and the study clearly emphasises the importance of rodents and shrews as hosts for immature stages of ticks, especially larvae. This means that they are thought to constitute important vertebrate hosts for the fulfilment of the life cycle of both *I. ricinus* and *I. trianguliceps* ticks. In relation to small rodents relatively few studies have previously investigated the role of shrews as host for tick (Nilsson, 1974; Humair et al., 1993; Bown et al., 2011). In the present study, *S. araneus* was the most abundant species and it was also found with relatively high infestation prevalence for both *I. ricinus* and *I. trianguliceps* larvae (Table 4 and 7), which might indicate that this species plays an important role in the life cycle of ticks on the west coast of Norway. Thus, it may also be important for the enzootic transmission cycle, as it has previously been proven as a competent reservoir for *A. phagocytophilum* in Great Britain (Bown et al., 2011). Host species trapped in the present study are likely to represent much of the small rodent and shrew diversity in the area, based on the distribution of small rodents and shrews on the west coast Norway (Østbye, 1994).

4.2.2 Extrinsic factors and seasonality

I observed that landscape variables had an effect on the occurrence of larval *I. ricinus* and *I. trianguliceps* infesting small mammals on the west coast for Norway. Climate parameters are major factors determining survival, distribution and activity of free-living ticks, and Brunner and Ostfeld (2008a) found that the abundance of questing ticks is an important predictor for tick burdens on hosts. Spatial variations in tick burdens on hosts are therefore thought to partly be explained by the free-living ticks' interaction with a heterogeneous environment. This has previously been supported by Paziewska et al. (2010) and Boyard et al. (2008). As predicted by the coast-inland/elevation tick abundance hypothesis (H1b), *I. ricinus* tick burdens on hosts decreased with increasing distance to the fjord (Fig. 3A), and were lower on hosts trapped in the more north-facing stations (Fig. 3B). This reflected the same pattern as I observed for the distribution of questing *I. ricinus* ticks in the same area, and is most likely due to lower temperature, restricting *I. ricinus* questing tick activity. This is in accordance with Rosà et al. (2007), which found that the tick burdens on hosts increased with increasing temperatures, likely as a consequence of increasing temperature on questing tick activity, previously observed by Randolph (2004) and Daniel et al. (2006). *I. trianguliceps* larval tick burdens was found to decrease with increasing elevation (Fig. 6B). Even though this species has been predicted to be a more robust tick species compared to *I. ricinus*, temperature has been found to highly affect the feeding activity of *I. trianguliceps* ticks. During an experimental study, Randolph (1975b) found that a decrease in temperature caused an increase in developmental time for *I. trianguliceps*. I therefore argue that the decrease in temperature at higher elevations could result in a longer development time of also free-living *I. trianguliceps* and thus fewer ticks are active, which could explain the results herein.

From the current study it was also evident that seasonality had the ability to affect tick burdens on hosts. This is in concordance with several other studies (e.g. Randolph, 1975b; Randolph, 2004; Brunner and Ostfeld, 2008a; Kiffner et al., 2010b), and has been linked to the effect of abiotic factors, such as temperature and humidity and seasonal fluctuations in host population densities. The highest *I. ricinus* larval infestation burdens on rodents and shrews were in early fall (Table 5), while *I. trianguliceps* larval infestation was found to be higher during the spring (Table 8). The results are partly in accordance with previous studies. *I. ricinus* have been found with both unimodal and bimodal peaks in North and Central Europe (Tälleklint and Jaenson, 1997; Randolph, 2004), while *I. trianguliceps* usually is found with bimodal pattern, with one small peak in early summer, followed by a higher peak

in autumn (Randolph, 1975b; Bown et al., 2003). Seasonal patterns have been shown to vary even at the same area between years, suggesting that studies of seasonal patterns should include several study years. In the current study, I cannot exclude that tick burdens might have peaked at a different time, as rodents and shrews were not captured repeatedly throughout the year.

4.2.3 Intrinsic factors

In the present study, I found that host factors affected the *I. ricinus* and *I. trianguliceps* tick burdens on hosts. The physical, behavioural and immunological characteristics of vertebrates are closely related to their quality as hosts, and likewise the differential distribution of ticks amongst them (Randolph, 2004; Brunner and Ostfeld, 2008a; Paziewska et al., 2010; Kiffner et al., 2010b). Individual attributes of hosts can thus provide valuable addition to the analyses of variation of tick burdens among hosts. Intrinsic factors have been shown to cause variation in tick burden among different host species, but also to cause striking variations within the same species. I observed a positive relationship between the number of ticks and the body size of hosts (H2), where heavier rodents and shrews were infested with a higher number of larvae and nymphs (Table 5, 6, 8 & 9). This observation is in concordance with previous studies from Europe (Perkins et al., 2003; Harrison et al., 2010; Kiffner et al., 2010b). The positive correlation was applicable for both species of ticks, however body size was not significant for *I. trianguliceps*. This might suggests that body size is less important for this species, as expected by the host selection-tick life stage hypothesis (H2b). *I. trianguliceps* is an endophilic (nest dwelling) tick. As such, immature rodents and shrews that spend a greater time in the proximity of the nest would have greater exposure to *I. trianguliceps* ticks (Bown et al., 2008), especially larvae.

Body size correlates with a number of other variables (e.g. species, sex and age), and most of these are in turn related to grooming rates, home range size, immune function and other factors, both within and between species. Thus it is clear that the effect of body size on tick burdens is very complex. The positive association between body size and tick burdens can be attributed to several different mechanisms (Perkins et al., 2003; Harrison et al., 2010). First and foremost tick burdens may correlate with host body size per see. This has been shown in a number of host-parasite systems (Arneberg et al., 1998), and may explain variation in tick burdens simply because large animals can offer a greater surface area for ectoparasites to target. Secondly, a size-dependent behaviour can explain the effect observed

by body size on the variation in tick burdens. Behavioural studies have shown that interspecific body size, where larger-sized species are found with higher mean infestation burdens, is because smaller host species groom (remove ticks) more (Mooring et al., 2000). This is based on the assumption that species of smaller size (with a large surface to mass ratio) cannot tolerate as great density of engorging ticks per unit body surface area as those of larger body size (Hart, 1990). This has later also been shown to apply for intraspecific relationships, where younger, smaller individuals groom at higher rates than older, larger individuals (Mooring and Hart, 1997). Grooming behaviour has been proved to be important in removal of ectoparasites in rodents (Murray, 1987; Shaw et al., 2003), however studies focusing on size and age dependent grooming behaviour in small mammals are scarce, and age was not included in the present study, as it was nearly impossible to distinguish age classes for the most abundant species, *S. araneus*. Thirdly, body size may also be attributed to a resource allocation trade-off, because of limiting resources (e.g., energy), which constrains both somatic growth and immune functions. In species where some individuals invest in enhanced growth, they do so at the expense of the immune system, thus making them more susceptible to parasites (Moore and Wilson, 2002). This mechanism has been posited as the ultimate explanations behind sex-bias parasitism in sex-dimorphic rodents (Perkins et al., 2003; Harrison et al., 2010). However, measuring energetic costs of maintaining a competent immune response is difficult and was outside the scope of this study. Given the number of mechanisms that can explain the positive correlation between body size and tick burdens it is impossible to infer from the current analyses the underlying process.

Although several studies have observed the same positive correlations between body size and tick burdens as presented here, there are some exceptions (Tälleklint and Jaenson, 1997; Brunner and Ostfeld, 2008a). The explanation for varied and conflicting results is that other host factors (e.g. host home range and host immunity) may affect tick burdens and that these factors may also change with age, sex, size and other unmeasured factors. I therefore also aimed to separate effects of species from body size differences by looking for residual effect of species after removing the body size factor. In the present study it is clear that there are some unmeasured quality of rodents and shrews species beyond body size affecting the burdens, especially for *I. ricinus* larvae (Table 5) and *I. trianguliceps* nymphs (Table 9). This may in turn affect the enzootic transmission cycle.

Home range size is related to the chance of encounter between ticks and their hosts in the habitat, and larger home ranges have been related to higher tick burdens (Randolph, 1975a; Tälleklint and Jaenson, 1997; Boyard et al., 2008; Devevey and Brisson, 2012;

Kovalevskii et al., 2013), and thus provide a mechanistic explanation for differences in tick burdens on individual hosts. However, any attempt to relate tick burdens to home range size of different hosts is difficult, and measuring of home range size was not feasible in a removal study, such as the present one. Individual variation in immune responses has also been shown to explain differences in tick burdens. High testosterone levels in male rodents have previously been shown to hamper the individual's immune response, resulting in higher tick burdens (Hughes and Randolph, 2001). Immune responses have also been suggested to explain variation in tick burdens between host species (Randolph, 1975a; Boyard et al., 2008; Paziewska et al., 2010; Kiffner et al., 2010b; Martello et al., 2014). Nevertheless, for most of the host species trapped in the present study there is, to my knowledge, no investigations on possible immune responses associated with tick attachment.

Additional variables, such as sex, age and home range could be favourable to increase the power of the analyses, to get a more holistic view of how the intrinsic factors affect the number of ticks on hosts. The role of intrinsic factors in explaining variation in tick burdens within and between small rodent and shrew species deserves further investigations given their potential affects for rodents and shrews contributions to the enzootic transmission cycle.

4.3 Tick-borne pathogens

Tick-borne pathogens can only be maintained in environments where the presence of vector-competent ticks and reservoir competent hosts overlaps (Radolf et al., 2012; Stuen et al., 2013). Knowledge of the reservoir competence of small mammals can give us a better understanding of the role these hosts play in the enzootic transmission cycle on the west coast of Norway. In the present study, small mammals were tested for *B. burgdorferi* s.l. and *A. phagocytophilum* but we did not separate different genotypes of either of the pathogens. As predicted by the host competence hypothesis (H3), both pathogens were detected in rodents and shrews.

Several species of mice, voles, rats and shrews have been shown to be competent reservoir of *B. burgdorferi* s.l., however the main reservoir hosts for *B. burgdorferi* s.l. in Europe have been considered to be *A. flavicollis*, *A. sylvaticus*, *A. agrarius*, and the vole *M. glareolus* (Gern and Humair, 2002). In the current study, 6.9% of the small mammals tested positive for *B. burgdorferi* s.l. (Fig. 9). The overall estimate of *B. burgdorferi* s.l. (6.9%) seems to be within the lower range typically reported in other studies from Europe (Humair et al., 1993; Sinski et al., 2006; Paulauskas et al., 2008; Gassner et al., 2013), but it was similar

to prevalence reported in an earlier study from Norway (Paulauskas et al., 2008). In Europe, *A. phagocytophilum* have been detected in several rodents such as *A. flavicollis*, *A. agrarius*, *A. sylvaticus*, *M. glareolus*, *M. agrestis* and in shrews (*S. araneus*) (Reviewed by; Stuen et al., 2013). In the current study, *A. phagocytophilum* were detected in 14.9% of the small mammals (Fig. 9). The overall prevalence for *A. phagocytophilum* was above the reported 1.6% from Slovakia (Blanarová et al., 2014), 5.3% in Germany (Hartelt et al., 2008) and 6.7% in England (Bown et al., 2006) and within the reported range 13.3 - 15% in Czech Republic (Hulínská et al., 2004). The results presented herein implies that small mammals, such as *M. agrestis*, *M. glareolus* and *S. araneus* are susceptible to infection of *B. burgdorferi* s.l. and *A. phagocytophilum*, however it does not provide us with a complete overview of the reservoir competence of these hosts. The reservoir competence is composed of the likelihood that the individual host can acquire the spirochetes from an infected tick bite, and the likelihood that this host if infected, are able to transmit the infection further to ticks feeding on it (Brunner et al., 2008b). Host species may vary dramatically in their propensity to transmit tick-borne pathogens to feeding ticks (Brunner et al., 2008b; Radzijevskaja et al., 2013) and their reservoir competence is best determined by transmission experiments in the laboratory (Brunner et al., 2008b).

Another area of which there is still little knowledge about, but can be important for the contribution of small mammals to the enzootic transmission cycle of several important pathogens is so-called epidemiological sub-cycles. In the current study, a large portion of the small mammals fed *I. ricinus* and *I. trianguliceps* larvae simultaneously (45.2%, n=252). Although *I. trianguliceps* is a nest dwelling species and associated primarily with rodents, the species could serve as a vector within the small mammal populations and thus leading to higher infection rates. Evidence of such a sub-cycle has been suggested for this tick species in the UK (Bown et al., 2006) and in Russia (Kovalevskii et al., 2013). Host sharing by the two species of ticks, as in the present study may increase the probability of *I. ricinus* to become infected and bridge the pathogens from the small mammals to humans. This together with relatively high infestation prevalence may confer to rodents and shrews in the present study an important status as potential reservoir hosts in the enzootic transmission cycle of ticks-borne pathogens. However, this field needs further research before we can obtain a holistic view of the importance of small mammals as reservoir for pathogens in this northern coastal forest ecosystem and on the specificity for pathogen genospecies.

5. Conclusions

In this study, I have made a number of novel observations that might have important implications for our understanding of the ecology of tick-borne pathogens at the northern distribution limit of ticks. One inference from the elevation gradients presented in the current study is that, as the climate gets warmer, an increase in tick abundance and range expansion at higher elevations might be expected on the west coast of Norway. Understanding of the extrinsic factors associated with the ecology of questing is important in our understanding of exposure to tick-borne pathogens with a changing climate.

The expansion of ticks and emergence of tick-borne pathogens is highly dependent on the composition and stability in the reservoir host community. The current study emphasizes the importance of rodents and shrews as host for immature stages of ticks, especially larvae. This indicates that they are important hosts contributing to the life cycle for both *I. ricinus* and *I. trianguliceps*, and may imply that they are important contributors to the enzootic transmission cycle. In this study, the use of GLMMs gave the opportunity to investigate trends in variation in tick burdens and I found that tick burdens appeared to be a consequence of a complex combination of extrinsic factors (like landscape variables), seasonality and intrinsic factors (like host body size, and other unmeasured host qualities). This suggests that some host individuals are more likely to contribute to the life cycle of ticks, and thus also to the enzootic transmission cycle than others. To better understand tick-borne diseases in relation to climate change, one should put more emphasis on tick burdens and the effect of intrinsic factors in future research.

This study is one of few studies that address the role of rodents and shrews as hosts for ticks in a northern ecosystem, and more research is needed to better understand the complex interaction between small mammals, ticks and pathogens. I suggest that further studies should focus on the link between small mammal and tick population dynamics in this ecosystem. This would, together with similar studies from other ecosystems increase the understanding of the role such hosts play in the ecology of ticks and tick-borne pathogens. In addition, it would be of interest to expand the current study by also including sex, age and home range of host species. All this may give us a more holistic view of the effect of intrinsic factors and the enzootic transmission cycle. Least but not last, the role of the two tick species as vectors should be further research in the present ecosystem as their specialisation may effect the role of rodents and shrews in the epidemiology of tick-borne pathogens.

6. References

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Appendix A – Questing tick abundance

Table 10. Model selection for the model explaining variation in abundance of questing *I. ricinus* ticks as a function of landscape variables and host abundance in Sogn & Fjordane county, Norway in 2013 – 2014. The best model is presented in bold fonts. X = term included in model

Model	Distance to fjord	Elevation	Slope	Northness	Season	Year	Total number of hosts	Season:elevation	Season:total number of hosts	Season:distance to fjord	AIC
1	x	x	x	x	x	x	x	-	-	-	276.478
2		x	x	x	x	x	x	-	-	-	274.52
3	x		x	x	x	x	x	-	-	-	278.02
4	x	x		x	x	x	x	-	-	-	274.536
5	x	x	x		x	x	x	-	-	-	279.72
6	x	x	x	x		x	x	-	-	-	275.88
7	x	x	x	x	x		x	-	-	-	274.75
8	x	x	x	x	x	x		-	-	-	276.276
9	-		x	x	x	x	x	-	-	-	288.142
10	-	x		x	x	x	x	-	-	-	272.566
11	-	x	x		x	x	x	-	-	-	277.754
12	-	x	x	x		x	x	-	-	-	273.88
13	-	x	x	x	x		x	-	-	-	272.822
14	-	x	x	x	x	x		-	-	-	274.28
15	-		-	x	x	x	x	-	-	-	286.152
16	-	x	-		x	x	x	-	-	-	275.77
17	-	x	-	x		x	x	-	-	-	271.962
18	-	x	-	x	x		x	-	-	-	271.004
19	-	x	-	x	x	x		-	-	-	272.306
20	-		-	x	x	-	x	-	-	-	284.16
21	-	x	-		x	-	x	-	-	-	273.772
22	-	x	-	x		-	x	-	-	-	270.35
23	-	x	-	x	x	-		-	-	-	270.878
24	-		-	x	-	-	x	-	-	-	282.3
25	-	x	-		-	-	x	-	-	-	273.856
26	**-**	**x**	**-**	**x**	**-**	**-**		**-**	**-**	**-**	**268.972**
27	-		-	x	-	-	-	-	-	-	281.17
28	-	x	-		-	-	-	-	-	-	273.27
29	-	x	-	x	x	-	-	x	-	-	269.8
30	-	x	-	x	x	-	x	-	x	-	272.022
31	x	x	-	x	x	-	-	-	-	x	271.694

Appendix B – *Ixodes ricinus* larva tick burdens

Table 11. Model selection for the model explaining variation in *I. ricinus* larvae tick burdens as a function of landscape variables and hosts factors in Sogn & Fjordane county, Norway in 2014. The best model is presented in bold fonts. X = term included in model.

Model	Host species	Log (body weight)	Elevation	Distance to fjord	Slope	Northness	Transect	Season	Transect:elevation	Transect:distance to fjord	AIC
1	x	x	x	x	x	x	x	x	-	-	1312.404
2		x	x	x	x	x	x	x	-	-	1331.47
3	x		x	x	x	x	x	x	-	-	1319.834
4	x	x		x	x	x	x	x	-	-	1310.556
5	x	x	x		x	x	x	x	-	-	1315.146
6	x	x	x	x		x	x	x	-	-	1312.402
7	x	x	x	x	x		x	x	-	-	1312.662
8	x	x	x	x	x	x		x	-	-	1312.086
9	x	x	x	x	x	x	x		-	-	1315.986
10		x	-	x	x	x	x	x	-	-	1329.56
11	x		-	x	x	x	x	x	-	-	1317.9
12	x	x	-		x	x	x	x	-	-	1315.648
13	x	x	-	x		x	x	x	-	-	1310.522
14	x	x	-	x	x		x	x	-	-	1311.78
15	**x**	**x**	**-**	**x**	**x**	**x**		**x**	**-**	**-**	**1310.316**
16	x	x	-	x	x	x	x		-	-	1314.148
17		x	-	x	x	x	-	x	-	-	1330.486
18	x		-	x	x	x	-	x	-	-	1318.314
19	x	x	-		x	x	-	x	-	-	1315.678
20	x	x	-	x		x	-	x	-	-	1311.414
21	x	x	-	x	x		-	x	-	-	1312.244
22	x	x	-	x	x	x	-		-	-	1314.084
23	x	x	x	x	x	x	x	x	x	-	1311.774
24	x	x	-	x	x	x	x	x		x	1310.606

Appendix C – *Ixodes ricinus* nymph tick burdens

Table 12. Model selection for the model explaining variation in *I. ricinus* nymph tick burdens as a function of landscape variables and host factors in Sogn & Fjordane county, Norway in 2014. The best model is presented in bold fonts. X = term included in model.

Model	Host species	Log (body weight)	Elevation	Distance to fjord	Slope	Northness	Transect	Season	AIC
1									120.0822
2	x								111.0424
3		**x**							**105.1576**
4			x						121.6908
5				x					119.835
6					x				121.8112
7						x			121.4434
8							x		120.9012
9								x	122.046
10	x	x							111.4074
11		x	x						105.889
12		x		x					106.2798
13		x			x				105.6052
14		x				x			106.9014
15		x					x		106.756
16		x						x	106.09

Appendix D – *Ixodes trianguliceps* larva tick burdens

Table 13. Model selection for the model explaining variation in *I. trianguliceps* larvae tick burdens a function of landscape variables and host factors in Sogn & Fjordane county, Norway in 2014. The best model is presented in bold fonts. X = term included in model.

Model	Host species	Log (body weight)	Elevation	Distance to fjord	Slope	Northness	Transect	Season	Transect: Elevation	Transect: Distance to fjord	AIC
1	x	x	x	x	x	x	x	x	-	-	1207.33
2		x	x	x	x	x	x	x	-	-	1205.656
3	x		x	x	x	x	x	x	-	-	1207.06
4	x	x		x	x	x	x	x	-	-	1207.918
5	x	x	x		x	x	x	x	-	-	1205.356
6	x	x	x	x		x	x	x	-	-	1221.704
7	x	x	x	x	x		x	x	-	-	1205.864
8	x	x	x	x	x	x		x	-	-	1205.878
9	x	x	x	x	x	x	x		-	-	1219.914
10		x	x	-	x	x	x	x	-	-	1203.672
11	x		x	-	x	x	x	x	-	-	1205.072
12	x	x		-	x	x	x	x	-	-	1207.676
13	x	x	x	-		x	x	x	-	-	1219.942
14	x	x	x	-	x		x	x	-	-	1203.864
15	x	x	x	-	x	x		x	-	-	1204.866
16	x	x	x	-	x	x	x		-	-	1217.92
17	-		x	-	x	x	x	x	-	-	1205.035
18	-	x		-	x	x	x	x	-	-	1205.61
19	-	x	x	-		x	x	x	-	-	1215.862
20	-	x	x	-	x		x	x	-	-	1202.564
21	-	x	x	-	x	x		x	-	-	1203.172
22	-	x	x	-	x	x	x		-	-	1217.392
23	-		x	-	x	-	x	x	-	-	1204.704
24	-	x		-	x	-	x	x	-	-	1203.64
25	-	x	x	-		-	x	x	-	-	1215.964
26	**-**	**x**	**x**	**-**	**x**	**-**		**x**	**-**	**-**	**1201.49**
27	-	x	x	-	x	-	x		-	-	1215.544
28	-		x	-	x	-	-	x	-	-	1203.312
29	-	x		-	x	-	-	x	-	-	1204.138
30	-	x	x	-		-	-	x	-	-	1214.322
31	-	x	x	-	x	-	-		-	-	1215.012
35	-	-	x	-	x	-	x	x	x	-	1204.564
36	-	-	x	x	x	-	x	x	-	x	1206.382

Appendix E – *Ixodes trianguliceps* nymph tick burdens

Table 14. Model selection for the model explaining variation in *I. trianguliceps* nymph tick burdens as a function of landscape variables and host factors in Sogn & Fjordane county, Norway in 2014. The best model is presented in bold fonts. X = term included in model.

Model	Host species	Log (body weight)	Elevation	Distance to fjord	Slope	Northness	Transect	Season	AIC
1	x	x	x	x	x	x	x	x	279.54
2		x	x	x	x	x	x	x	280.538
3	x		x	x	x	x	x	x	279.084
4	x	x		x	x	x	x	x	278.156
5	x	x	x		x	x	x	x	277.548
6	x	x	x	x		x	x	x	277.768
7	x	x	x	x	x		x	x	277.612
8	x	x	x	x	x	x		x	278.432
9	x	x	x	x	x	x	x		277.634
10		x	x	-	x	x	x	x	278.578
11	x		x	-	x	x	x	x	277.092
12	x	x		-	x	x	x	x	276.836
13	x	x	x	-		x	x	x	275.808
14	x	x	x	-	x		x	x	275.63
15	x	x	x	-	x	x		x	279.802
16	x	x	x	-	x	x	x		275.64
17		x	x	-	x	-	x	x	276.772
18	x		x	-	x	-	x	x	275.25
19	x	x		-	x	-	x	x	274.898
20	x	x	x	-		-	x	x	273.93
21	x	x	x	-	x	-		x	277.972
22	x	x	x	-	x	-	x		273.718
23		x	x	-	x	-	x	-	274.858
24	x		x	-	x	-	x	-	274.242
25	x	x		-	x	-	x	-	272.94
26	x	x	x	-		-	x	-	272.026
27	x	x	x	-	x	-		-	276.054
28		x	x	-	-	-	x	-	273.014
29	x		x	-	-	-	x	-	272.636
30	**x**	**x**		**-**	**-**	**-**	**x**	**-**	**271.518**
31	x	x	x	-	-	-		-	274.216
32		x	-	-	-	-	x	-	273.91
33	x		-	-	-	-	x	-	273.326
34	x	x	-	-	-	-		-	274.93